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## The Relationships of the West Indian Species of *Aratinga* (Aves, Psittacidae)

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### INTRODUCTION

The parakeet genus *Aratinga* Spix was investigated, as part of a larger study of West Indian zoogeography, in an attempt to reconstruct in so far as possible its history in the islands. It was soon found that the study must include many of the members of the genus besides the West Indian representatives and their apparent mainland relatives.

Although much progress has been made within the last two decades in bringing up to date our knowledge of the rich Neotropical avifauna, thanks largely to the studies of Zimmer, Phelps, de Schauensee, and others, the majority of this work is of a regional nature. Perhaps the time is now approaching for systematic reviews of single groups of South and Middle American birds at a level above that of the species. Particularly among the New World parrots are such revisions needed, to integrate the evidence of the newer faunal studies with modern points of view. Many species have been revised piecemeal in the course of previous faunal studies, without regard in general to other members of the genus or even other subspecies far removed from the localities of interest to the reviser. New subspecies have been described without adequate consideration of the species as a whole.

The inadequacy of knowledge of the taxonomy of American parrots became apparent as the result of the effort to determine in more detail the exact origins, in point of geography and taxonomic entity, of the West Indian parrots and parakeets. Although the lack of any recent review of these groups proved a handicap in this study, no attempt at a formal revision of species and subspecies has been made. In fact,

taxonomic status (i.e., whether a form is a full species or not), the finer details of distribution, and nomenclature are here considered definitely secondary to the main problem of general affinities. We have tried, nevertheless, to point out the more important gaps in our knowledge and to suggest where further study and collecting are most apt to advance our understanding of the systematics of this group.

Parakeets of the genus *Aratinga* have been among the relatively few psittaciform birds to colonize the West Indies, the others having been the macaws (*Ara*), possibly *Anodorhynchus*, and the large parrots of the genus *Amazona*. All three genera (*Ara*, *Aratinga*, and *Amazona*) include numerous species of which the aggregate distributional area is very extensive. They occupy ranges from northern Argentina to Mexico, and it is not surprising that such adaptable and far-ranging birds should also have reached the Antilles. None of these genera has received treatment in the form of a comprehensive review; the closest approach was Peters' arrangement of the species for his check list.

The parakeets now included in the genus *Aratinga* were formerly divided among three genera, namely, *Thectocercus*, *Aratinga*, and *Eupsittula*. In spite of the fact that they can be easily included in the single, larger genus (perhaps even *Ara* should not be excluded), they are natural subgroups, possibly subgenera. Only species of what we call the subgenera *Aratinga* and *Eupsittula* are involved in the colonization of the West Indies.

### THE WEST INDIAN SPECIES

The forms of *Aratinga* represented in the West Indies are:

*Aratinga* (*Eupsittula*) *nana* Vigors. Jamaica.

*Aratinga* (*Eupsittula*) *pertinax pertinax* Linnaeus. St. Thomas, Virgin Islands. Usually assumed to have been introduced from Curaçao.

*Aratinga* (*Aratinga*) *chloroptera chloroptera* Souancé. Hispaniola.

*Aratinga* (*Aratinga*) *chloroptera maugei* Souancé. Known only from Mona Island between Hispaniola and Puerto Rico; may have occurred on Puerto Rico (Wetmore, 1916; Wetmore and Swales, 1931). Extinct?

*Aratinga* (*Aratinga*) *euops* Wagler. Cuba; formerly also Isle of Pines but now extinct there.

*Aratinga* (*Aratinga*) *labati* Rothschild. Formerly Guadeloupe, now extinct. No specimens known; the name is based on the writings of Labat (Rothschild, 1905). Possibly occurred on other islands in the Lesser Antilles. Ridgway (1916) tentatively put this form in the genus *Eupsittula*, but it appears to have been a typical *Aratinga* in color pattern.

Each of the above species represents a separate colonization of the West Indies, with the probable exception of *A. chloroptera* and *A. euops* the divergence of which may well have taken place within the Greater

Antilles. Each of these invasions poses somewhat different problems, and the degree of confidence to be placed in our postulated routes is quite different in each case. Because of these differences, a critical discussion of the separate colonizations is made in turn.

### ARATINGA NANA

There is no special problem involved in the derivation of *Aratinga* (*Eupsittula*) *nana* of Jamaica, as it is obviously most closely related to *A. (Eupsittula) astec* of the Caribbean slope of Central America. Indeed, Bond (1945) considered the two to be conspecific, the older name being *nana*. We are inclined to agree with Bond for several reasons, derived from a survey of how similar sympatric species of this subgenus can be, and how different the accepted subspecies of species within the subgenus can be.

In this connection, the most pertinent evidence would be that afforded by *A. astec* itself. Peters (1937) admits two subspecies: the nominate race of the Caribbean slope of Mexico and Central America to western Panama, and *A. astec vicinalis* Bangs and Penard (1919) of southern Tamaulipas. We have seen only two specimens of the latter form, and these we have compared with specimens of the nominate subspecies. Despite the statement of Bangs and Penard that their new race is quite distinct, our two specimens are exceedingly similar to *A. a. astec*. With such limited material, a comparison of the degree of difference between the races of *A. astec* and *A. nana* cannot fairly be made. The Jamaica form is larger than *A. astec*, somewhat darker, and tends to lack the yellow feathering on the cere usually present on the mainland form. However, many specimens of *A. nana* do show traces of such yellow feathering. Thus we are forced to consider some other, indirect, evidence based on related species.

We next examined the numerous subspecies of *A. (Eupsittula) pertinax*. We found that *A. nana* and *A. astec* are more similar to each other than some of the recognized races of *A. pertinax* are to one another.

It is our opinion that *A. astec* and *A. nana* are much more like each other than the members of any one of the groups of sympatric species of the subgenus *Eupsittula* are like one another. In other words, there are greater differences among the species *A. auricapillus*, *A. cactorum*, and *A. aurea*, or between *A. pertinax* and *A. solstitialis*, for example, than between *A. astec* and *A. nana*. Furthermore, there are fewer differences between these two forms than differences among *A. jandaya*, *A. solstitialis*, and *A. auricapillus*, which Peters (1937) mentioned as probably conspecific.

Whether or not *A. nana* and *A. astec* are conspecific is, however, immaterial to the problem of the derivation of the Jamaica form. In either case, there seems little doubt that *A. nana* was derived directly from Middle America. That this event might have taken place relatively recently is indicated primarily by the fact that *A. nana* is so little different from *A. astec*. Of secondary consideration is the presence of *A. nana* on Jamaica alone of the Greater Antilles; one possible explanation of this distribution is that lack of sufficient time has limited the extension of range.

#### ARATINGA PERTINAX

It is generally thought that the presence of this parakeet on St. Thomas is to be explained by its introduction from Curaçao, but this is merely an assumption based on probabilities rather than positive evidence. Because other disciplines, such as anthropology and geology, often employ faunistic evidence in evaluating their hypotheses, it may be well to state the problem in a little more detail than it might otherwise merit.

The only ascertainable facts at present concern the relationships of the birds as shown by their morphological resemblances. In color pattern, the Antillean population is apparently identical with birds from Curaçao (nominate *pertinax*). Birds from the neighboring island of Bonaire (*A. p. xanthogenia* Bonaparte) have been characterized as having the whole of the head yellow in the adult, whereas the birds from Curaçao and St. Thomas have only the forehead yellow. However, adults from the latter islands are indistinguishable in color from immatures of either race. The only other form approaching these in color is *A. p. surinama* Zimmer and Phelps (1951) from eastern Venezuela, Surinam, and Cayenne, but that form is more like brown-cheeked continental populations. The resident race on Aruba, *A. p. arubensis* Hartert, is somewhat intermediate between mainland and island races, but much closer to *A. p. aeruginosa* Linnaeus of western Colombia than it is to Curaçao birds.

However, birds from St. Thomas and Curaçao, as well as birds from Bonaire, are not identical. Apart from the color differences between those of Bonaire, and those of Curaçao and St. Thomas, measurements indicate the possible existence of small size differences among the three populations.

The following measurements (in mm.) were made on specimens in the American Museum collection, taken on St. Thomas by Rollo Beck in August and September, 1916. All the birds were in molt, but figures

are given for those that appeared to have full-grown remiges and rectrices. Wing, males: 140, 140, 140, 140, 140, 140, 140, 136, 135; females: 138, 137, 136, 136, 133; tail, males: 127, 123, 120, 120, 117, 116, 113; females: 123, 112, 111, 109; bill (from cere), males: 20, 20, 20, 20, 19.5, 19, 19, 19, 18, 18, 18; females: 19.5, 19, 19, 18, 18, 18. Immatures are indistinguishable from adults in color, but if the evidence from a series from Bonaire is valid (see below), then some of the smaller specimens may represent juveniles.

Four worn specimens from Curaçao measure: wing, males: 145, 142; females: 143, 140; tail, males: 128, 109; females: 122, 121; bill, males: 21, 20; females: 19, 17. Worn birds, such as these, would be expected to be somewhat smaller than freshly molted birds but it is also possible that the fresh feathers of the birds from St. Thomas were not full grown. According to the collector's label, the small female of this series is a juvenile. Ridgway's (1916) measurements also show a small size difference between specimens from Curaçao and those from St. Thomas.

Worn specimens from Bonaire measure as follows: wing, adult males: 151, 143, 140; juvenile males: 142, 139; adult females: 143, 138; juvenile female: 140; tail, adult males: 134, 123, 120; juvenile males: 119, 115; adult females: 115, 110; juvenile female: 113; bill, adult males: 22, 22, 22; juvenile males: 21, 20; adult females: 21.5, 20; juvenile female: 19.5. Juveniles are listed as such when so identified by the collector, in this case Hartert. All these juveniles have only the forehead yellow, although two specimens not recorded as being immature also have the yellow restricted to the forehead. It would seem, therefore, that Hartert was not relying solely upon crown color as an age criterion. The juveniles are smaller in tail and bill lengths, but not obviously so in wing length.

While the number of specimens is insufficient to establish size differences clearly, they suggest at least a mean that is highest in all measurements for birds from Bonaire, an intermediate figure for those from Curaçao, and a size that is smallest for birds from St. Thomas. Hartert (1893) noted that Bonaire specimens seemed to be slightly larger than those from Curaçao, especially in culmen length.

The distinctions among these three populations are weak at best. While it therefore appears that *A. pertinax* on St. Thomas is closest to the indigenous form of Curaçao, Bonaire is not completely eliminated from consideration as a possible, but highly unlikely, source of the Antillean population.

At least three reasonable hypotheses suggest themselves as to the origin of the parakeet on St. Thomas.

1. The curious distribution (St. Thomas and Curaçao) suggests, of course, human introduction on St. Thomas, as the major part of the range of *A. pertinax* is northern South America. If the birds of St. Thomas should prove to be smaller than those of Curaçao, it would indicate a relatively earlier introduction, if such there was, than is implied by the belief that they are identical with birds from Curaçao.

2. Direct natural over-water transportation from Curaçao to St. Thomas (either by natural flight or by hurricane) is a second possibility. Hartert (1893) has pointed out that several unrelated and quite different species and subspecies have a similar distribution pattern. This would fit into G. G. Simpson's concept of a "sweepstakes route." It would seem rather unlikely that all these forms (those cited by Hartert and *A. pertinax*) were introduced by either Carib Indians or Europeans from Curaçao or Bonaire to the Greater Antilles alone and not be represented at all in the Lesser Antilles. In these cases, the Curaçao-Bonaire and the Greater Antilles forms are sometimes slightly different, indicating some evolutionary divergences. A size difference (if it exists) between the population of *A. pertinax* on Curaçao and that on St. Thomas may be due to the fact that smaller birds constituted the foundation stock on St. Thomas, that is, a chance event in the original colonization with no subsequent evolution. If such a possible size difference was not due to chance and a recognizable degree of morphological evolution occurred since the original colonization, an earlier derivation, perhaps in pre-Columbian times, is suggested. Evolutionary change of such a small degree in less than 500 years, however, is not theoretically impossible in insular populations.

An illuminating recent study is that by Ashton and Zuckerman (1950, 1951a, 1951b) on a population of green monkeys isolated on St. Kitts for 300 years. This introduced population has apparently become significantly different from the ancestral African form in several quantitative cranial characters in the intervening period.

3. It is also possible that this species worked its way up through the Lesser Antilles and is now extinct everywhere else in the archipelago. This seems to us to be the least satisfactory hypothesis. First, it requires the supposition of extinctions of populations which are not known to have existed. Second, although, according to Clark (1905), it is not improbable that a population of *A. pertinax* once existed on Martinique, this population seems to have been of a kind different from the nominate form of Curaçao and St. Thomas. This information is derived from Brisson, who referred to a plate of Edwards representing *A. pertinax aeruginosa* Linnaeus (Clark, 1905). That race now occurs

in the Caribbean portion of Colombia, western Venezuela, and north-western Brazil. Third, except on Curaçao, the populations now geographically nearest to the Lesser Antilles are not like the St. Thomas population. Thus, if this third hypothesis is correct, either the end members of the postulated insular series have independently evolved away from a brown-cheeked condition, such as is now present on the South American continent and was presumably present on Martinique, to the yellow-cheeked condition, or, conversely, the continental and Martinique populations convergently evolved into brown-cheeked forms.

Currently there is no way to decide the issue, and it must remain open. In our opinion, the third suggestion requires a greater number of assumptions and is therefore not the one of choice. On the other hand, it should be recognized that the introduction theory is at least as probable as a theory of natural over-water dispersal, if we consider both the evidence of other species with a similar distribution pattern and the possible mensural differences. It seems to us, furthermore, that, if there was a parakeet on Martinique resembling *A. p. aeruginosa*, there may have been at least two separate colonizations or introductions of *A. pertinax* into the West Indies, originating from different continental populations.

### *ARATINGA EUOPS*, *ARATINGA CHLOROPTERA*, AND *ARATINGA LABATI*

#### THE PROBLEM

The origin, or origins, of the Antillean members of the subgenus *Aratinga* are not immediately obvious. *Aratinga euops* and *A. chloroptera* agree so closely in most characters, except size, that it seems very probable that they arose from a common stock. *Aratinga labati*, however, seems to have been more distinct; it is therefore by no means clear whether or not one or two invasions of the West Indies are involved.

As is shown below, *A. euops* and *A. chloroptera* are close by simple character comparisons to *A. leucophthalmus* of the Amazon and Orinoco valleys. Likewise, *A. labati* appears to have resembled most closely *A. holochlora* of Mexico and northern Central America. In each case, however, a wide geographical hiatus exists between the insular forms and the mainland populations most like them. The intervening areas are inhabited by related forms, with different color character combinations. It is difficult to believe, therefore, that the superficial resem-

blances are indicative of true affinity, as this would imply either several mass extinctions and recolonizations or direct dispersal across very wide water gaps. Clearly some simpler hypotheses consistent with the facts of morphology and distribution would be preferable. It was felt necessary to analyze in greater detail the characters, variation, and distribution of the subgenus *Aratinga* to see whether or not the Cuban and Hispaniolan forms in particular could have come from near-by Middle America.

#### MATERIALS AND METHODS

The species listed by Peters (1937) here considered to belong to the subgenus *Aratinga* are: *holochlora* Sclater, *strenua* Ridgway, *finschi* Salvin, *wagleri* Gray, *mitrata* Tschudi, *erythrogenys* Lesson, *leucophthalmus* P. L. S. Müller, *euops* Wagler, *chloroptera* Souancé, *labati* Rothschild, and *guarouba* Gmelin. *Aratinga strenua*, however, frequently is considered to be a race of *A. holochlora*, as in the Mexican check list by Friedmann, Griscom, and Moore (1950). In any case, with the exception of *A. guarouba*, all the "species" are apparently allopatric (but see Discussion), and we are at most dealing with one superspecies or even one geographically variable and widespread species. *Aratinga guarouba* of Amazonia is much larger, and with its striking yellow body and green wings seems at first sight to have a color pattern very different from that of the more typical members of the subgenus. Inspection of the *auricapillus-jandaya-solstitialis* group of the subgenus *Eupsittula* shows how the development of a similar color pattern might have occurred, for in this group the intermediate forms are known. There seems no reason, therefore, for not including *A. guarouba* in the subgenus *Aratinga*; its color pattern is the same as that of the other members, but the loss of structural blue everywhere except on the wings has exposed the xanthochromes. *Aratinga guarouba* is not here discussed further. A revision of the group would be rewarding, as the last listing by Peters is apparently in large part a compilation of outdated faunal works.

These conures are essentially birds of tropical and subtropical forest ranging from Sonora and Tamaulipas in Mexico south through Central America and South America to northern Argentina and Uruguay, and the West Indies. They are about the size of an American robin (*Turdus migratorius*), with a fairly long, graduated tail, in general color green, but red may appear in various parts of the body and wing plumage.

With the exception noted below, all specimens examined are in the collection of the American Museum of Natural History and number

approximately 280. One of us (Koopman) has seen a specimen of *A. chloroptera maugei* Souancé, and compared it with a large series of *A. c. chloroptera*, at the Chicago Natural History Museum. Examples of all the subspecies formally listed by Peters were examined except the following three, two of which have been described since 1937: *A. holochlora brewsteri* Nelson (Sonora), *A. wagleri minor* Carriker (upper Marañon Valley, Peru), and *A. leucophthalmus nicefori* de Schauensee (Guaicaramo, Colombia).

The characters that distinguish the species are, other than size, the presence or absence and amount of red on the crown, cheeks, throat, under wing-coverts, and tibiotarsus, and the color of the primary under wing-coverts. Each species and subspecies was examined to determine the characters and the extent of variability. Geographic variation and the distribution of these characters among the species were then analyzed by comparison of the species with one another.

#### CHARACTER ANALYSIS

There is much individual variation in these birds, and the distribution of color in the different forms is best presented in tabular form (table 1). This table should be compared with the generalized distribution map (fig. 1). The names used follow those of Peters for convenience, but they undoubtedly do not reflect in all cases the true relationships and rather should be thought of as indicating the geographic distributions of the characters, as no two species occur together.

The sexes are seemingly alike in coloration. Some of the observed variation may, however, be due to age differences. Young birds are mostly or entirely green, but some juvenile birds may have red in the plumage in those forms in which the adults have red (see, for example, Ridgway, 1916). Few of the specimens examined were labeled as to age, and thus one task was to separate adult and immature birds. Because size and color have been used in the analysis of geographic variation, an attempt was made to find some independent means of determining the age of the specimens. Unfortunately, we have been unable to obtain any reliable criterion. Attenuation of the rectrices, often used in passerines, appears to be of little value in *Aratinga*. We are forced to consider color and size as clues to age, with the understanding that they have not been confirmed in value by independent tests. A number of specimens of species other than the all green *A. holochlora* were consistent in having very little or no red on the body, and, in the case of *A. leucophthalmus*, olive rather than yellow primary under wing-coverts. Some but not all of these same specimens were

TABLE 1  
DISTRIBUTION OF CHARACTERS IN THE SUBGENUS *Arainga*

Form	Crown	Cheeks	Red in Body Throat	Legs	Back	Belly	Red	Under Wing-Coverts Olive	Yellow
<i>h. holochlora</i>	Traces	—	Traces <sup>a</sup>	—	—	Traces <sup>a</sup>	—	+	—
<i>h. brevipes</i>	—	—	—	—	—	—	—	+	—
<i>h. rubritorquis</i>	Traces	—	+ <sup>a, b</sup>	Traces	—	Traces	Trace	+	—
<i>strenua</i>	Traces	—	Traces	—	—	—	—	+	—
<i>euops</i>	Scattered	Scattered	Scattered	Traces	Scattered	Traces	+	+	—
<i>chloroptera</i>	—	—	—	—	—	—	+	+	—
<i>erythrogenys</i>	+	+	—	+	—	—	+	+	—
<i>m. mitrata</i>	+	+	—	+	Traces	Traces	—	+	—
<i>w. wagleri</i>	+	—	—	+	—	Traces	Trace	+	—
<i>w. transilis</i>	+	—	—	Traces	—	—	—	+	—
<i>l. leucophthalmus</i>	Traces	Scattered	Traces	Traces	—	—	+	—	+
<i>l. callogenys</i>	Traces	Scattered	+ <sup>b</sup>	Traces	Traces	—	+	— <sup>b</sup>	+ <sup>b</sup>
<i>finschi</i>	+	Traces	Traces	Traces	—	—	+	+ <sup>b</sup>	+ <sup>b</sup>
<i>labati</i>	(Traces)	(—)	(—)	(—)	(—)	(—)	(—)	(+)	(—)

<sup>a</sup>Orange-yellow.

<sup>b</sup>Very variable.

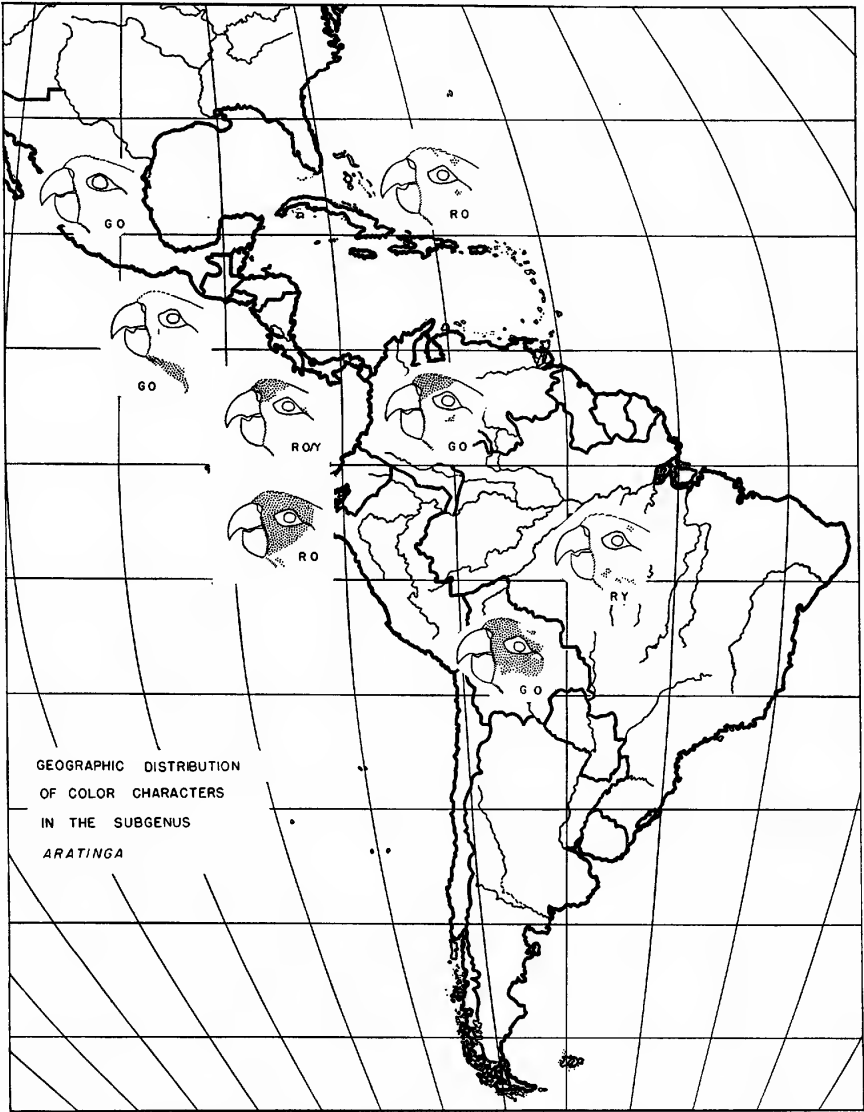


FIG. 1. Map of geographic distribution of color characters in the subgenus *Aratinga*. Stippled pattern indicates red color; absence of stippling indicates green color (except on bill). Lettering indicates color of under wing-coverts, primary under wing-coverts being listed second. G, green; O, olive; R, red; Y, yellow. On left, from north to south: *holochlora* subspecies; *holochlora rubritorquis*, *finschi*, *erythrogenys*, and *mitrata*. On right, from north to south: *euops*, *wagleri*, and *leucophthalmus*.

also of small size. It is believed that such birds were no older than one year when collected, although the inference is not proved. In the study of geographic variation, specimens with very little red but not necessarily of small size were not considered.

Other parrots, such as *Amazona*, are stated to show increasing amounts of red with advancing age even after reaching sexual maturity (Blake, 1953); perhaps this is also true for *Aratinga*. Clearly in such a situation it would be impossible always to distinguish variation due to age from other sources of variation when one is dealing with museum specimens of unknown age. By the removal of specimens that gave the greatest indication of being immature, we feel that the residue of possibly young birds does not contribute substantially to the observed variation.

Other sources of non-genetic variation are condition of the plumage (whether fresh or worn) and seasonal differences. There are no obvious seasonal differences in the plumage nor does wear appear to affect the amount of red. Diet, known to affect the expression of pigment in captive parrots, is perhaps a factor in the variability of wild birds.

Although it is entirely possible that we have underestimated the contribution of non-hereditary sources of variation, it would be reasonable to expect that some of the observed individual differences can be attributed to individual differences of genetic constitution.

Turning to the main trends, we find the following:

Red on the forehead is characteristic of birds in western South America from Venezuela and Colombia south to northern Argentina along the Cordilleras (*A. wagleri*, *A. mitrata*, and *A. erythrogenys*); in Central America from southern Nicaragua to western Panama (*A. finschi*). Only in *A. erythrogenys* and *A. mitrata* does the red of the crown extend downward to cover the cheeks; in the latter species there is apparently a clinal decrease in red on the cheeks from Argentina northward to Peru. Red is restricted to the forehead in *A. wagleri*, there being a distinct green stripe on the lores and above the eye.

A red throat is well developed only in the birds of Central America from eastern Guatemala to northern Nicaragua (*A. holochlora rubritorquis*). *Aratinga leucophthalmus callogenys* of northwestern Amazonia is the only other form to have numerous red feathers on the lower cheek and throat, but only one bird that we have seen has a solidly red throat. The Middle American bird, however, is orange-red; the Amazonian bird is scarlet. Occasionally, in specimens of other species with red crowns and cheeks, the red extends somewhat onto the throat, but this is not the usual condition.

The South American Cordilleran species with red foreheads have red tibiotarsi. However, some red feathers on the shanks appear in nearly all the forms except the all-green Middle American ones.

Red under wing-coverts are to be found in the following geographical regions: the Greater Antilles (*A. euops*, *A. chloroptera*); southern Central America (*A. finschi*); eastern South America (*A. leucophthalmus*); and the arid zone of northwestern Peru and southwest Ecuador (*A. erythrogenys*). The primary under wing-coverts are always yellow in *A. leucophthalmus*. In *A. finschi*, these feathers tend to be all yellow, but some specimens have both yellow and olive feathers. The primary under wing-coverts are olive in all the other species except *A. chloroptera maugei* in which they are pink. In some individuals of *A. c. chloroptera*, some of the primary under wing-coverts are pink, but never all of them.

There are occasionally red feathers in the body plumage of many of the forms, but they are most consistently present in the Cuban *A. euops*.

The variability appears to be mostly intrapopulational, that is to say, not due to possible interbreeding between some of the "species." It appears, however, that the insular forms, such as *A. holochlora brevipes* from Socorro Island off the west coast of Mexico, *A. chloroptera*, and *A. euops* are somewhat less variable than the continental populations. This suggests that the variability of the mainland birds might be at least partly due to interbreeding.

The distribution of the color characters shows no obvious correlations with the environment in a broad sense. Thus, although these parakeets live in several different biotic zones, the same characters may appear in different zones, and different characters be present in similar zones. For example, *A. erythrogenys* is a bird of the arid tropical zone in western Ecuador and Peru; *A. wagleri* inhabits the wet tropical zone. Both forms have red on the head, but the former has red under wing-coverts, a character it shares with the wet tropical zone *A. leucophthalmus*. But the wet tropical forest species, *A. wagleri* on the one hand and *A. leucophthalmus* on the other hand, have exactly opposite combinations of characters. It would seem that the color characteristics are related to local selective forces within the broader aspects of the environment. Color pattern possibly may be related to the presence of somewhat similar-appearing parakeets in the same area and serve as recognition marks. Within the subgenus *Aratinga*, in those forms of which the ranges are contiguous or nearly so, there are distinctive combinations of head and under wing-covert color pattern. These may

be a part of reproductive isolating mechanisms, if such in fact do exist.

The Greater Antillean species differ from their nearest mainland relatives chiefly in the color of the under wing-coverts, in which character they resemble two of the South American forms and the southern Central American bird, *A. finschi*. They differ from the latter and *A. erythrogenys* in lacking a red forehead, and from *A. leucophthalmus* in lacking yellow primary under wing-coverts.

The Cuban species, *A. euops*, can be recognized at once by its small wing length. The Hispaniolan species, *A. chloroptera*, is similar to *A. euops*, but larger and without interspersed red feathers in the body plumage; it can be separated from all other forms by the combination of green head, red under wing-coverts, and olive primary under wing-coverts.

On the whole, then, the Greater Antillean species are not conspicuously more similar to any one particular form than to another in the subgenus *Aratinga*, although the combination of red under wing-coverts and green head strikes one as being most like that of *A. l. leucophthalmus* which ranges north in eastern South America approximately to the Orinoco Valley.

#### *Aratinga labati*

Before the problem of the derivation of the Greater Antillean species of the subgenus *Aratinga* is considered, the status of "*Aratinga labati*" must be discussed. Because *Aratinga* (*sensu stricto*), if it did in fact exist there, must have become extinct in the Lesser Antilles quite early in the history of ornithological work on American birds, and because no pertinent fossil material has been described, the only record consists of reports of early travelers. Of these reports, one of the few of any value in identifying the forms involved is the account of Père Labat (1724). This account is mentioned by Clark (1905) and formed the basis of the erroneous description of *Conurus labati* by Rothschild (1905).

That Labat evidently knew the bird well in life is shown by his clear distinction of parakeets from both *Ara* and *Amazona*, and by his descriptions of feeding and other behavior in both wild and captive birds. His account of the parakeet, although short, therefore would appear to be worthy of credence. In one of the 1724 editions of his work,<sup>1</sup> which we have examined, there is even a crude plate on page 154

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<sup>1</sup> There are four editions of Labat's book, beginning in 1722. Clark, Rothschild, and Ridgway refer to the last, or 1742, edition, with the pertinent passages appearing on page 218. We have seen only the two 1724 editions; the texts of both are identical, but only one of these has a plate illustrating the parrots.

illustrating the three genera of psittaciform birds from the French islands. There can be no doubt of his having observed a small parakeet.

He describes the parakeet as follows: "On appelle perrique la troisième espece des perroquets. Elles sont toutes très-petites, & c'est en partie leur petitesse qui fait leur beauté. Celle de la Guadeloupe sont à peu près de la grosseur d'un merle, toutes vertes, excepte quelques petites plumes rouge qu'elles ont sur la tête. Leur bec est blanc; . . ." From this statement and the plate it is clear that we have a long-tailed, all-green parakeet with a few red feathers on the head (somewhat like *A. euops* from Cuba) and presumably not aggregated into a distinct red crown patch, as incorrectly stated by Rothschild (1905). No mention is made of any red patch on the wing, although if this were present it is hard to believe that Labat could have overlooked it while at the same time noting the detail of the few red feathers on the head. It is reported that this wing patch is conspicuous when the bird which possesses one is in flight (Wetmore and Swales, 1931). (Although Labat compared the Antillean parakeet with a bird from Brazil with which he was familiar, the latter would appear not to have been an *Aratinga*. Possibly he had in mind *Brotogeris*; he noted the Brazilian bird as having a fine white bloom on the feathers, thereby appearing silvery-green. Again, no mention is made of any red wing patches.)

Can the Guadeloupe parakeet be identified with any known parakeet from neighboring regions? Its size, that of a European blackbird, and its wholly green color appear to rule out all long-tailed parakeets except a member of the subgenus *Aratinga*. Ridgway's (1916) tentative assignment of it to *Eupsittula* has no real basis. It agrees best with *A. holochlora* except for the small red feathers mentioned as being on the head, which is not a usual condition in that species (*A. h. rubritorquis* has a red throat patch).

Because the ranges of *A. holochlora* and *A. labati* are so widely separated, and because of the slight difference of color pattern, *A. labati* is best considered a locally differentiated form. Its origin is considered below in connection with the problems raised by the two Greater Antillean species. It should be remembered that the only other extinct, Lesser Antillean parakeet of which we have any information, that from Martinique, was apparently a *Eupsittula* related to *A. pertinax*.

#### DISCUSSION

We believe that the taxonomic color characters within this subgenus probably have a relatively simple genetic basis, because they involve chiefly recombinations of a small number of distinctive color differ-

ences. However, the extent of observed variation suggests the presence of additional genetic and environmental modifying factors. With this in mind, the disjunct distribution of the characters in these obviously very closely related forms is less surprising than may seem at first sight. It appears not improbable that characters such as a red crown or red under wing-coverts could have been independently evolved in different populations of *Aratinga*. Alternatively they may represent independent retentions of primitive characters. Even now, in some populations the kind of variation, if it is genetic, may be adequate to bring about the formation of new constellations of characters of a similar sort. For example, *A. holochlora* and *A. leucophthalmus* (species which are essentially green-crowned) have many individuals with red feathers interspersed throughout the head region. (These, it should be noted, cannot be considered immature birds.) In any case, the hypothesis of independent evolution does not stand or fall on the kind and degree of intrapopulational variation.

From the distribution of color characters in living populations, it seems probable that several primary differentiation centers appeared soon after the original dispersal of the ancestral stock of the subgenus *Aratinga*. These differentiation centers seem to have been:

1. Eastern South America: green forehead, red and yellow under wing-coverts.
- 2a. Southeastern Peru to northwestern Argentina, eastern slopes of the Andes: red forehead and cheeks, olive under wing-coverts.
- 2b. Western Colombia and northern Venezuela: red forehead, green cheeks, and olive under wing-coverts.
3. Possibly another center was established in the arid coastal region of southwestern Ecuador and northwestern Peru: red crown and red cheeks, red and olive under wing-coverts.
4. Caribbean coast from western Panama to southern Nicaragua: red forehead, red and yellow or olive under wing-coverts.
5. Northern Central America and Mexico: green forehead and olive under wing-coverts.
6. Cuba and Hispaniola: green forehead, red and olive under wing-coverts.
7. Possibly still another center in the Lesser Antilles (Guadeloupe): morphologically quite similar to (5).

These particular color patterns are not peculiar to *Aratinga*; there are other Neotropical parrot genera with red foreheads or red under wing-coverts or both. Of course these other genera differ from *Aratinga* in details of the plumage. It suggests, however, that parallelism in color pattern is not uncommon in this family of birds and that resemblances need not necessarily imply direct relationships. This may be especially true in forms scarcely above the subspecific level of differen-

tiation. Normally, in the absence of reasons to believe otherwise, degree of resemblance is taken to indicate degree of relationship. As is well known, however, closely related subspecies developing on ecologically similar but geographically separated areas often tend to resemble one another closely in certain morphological features. This is usually recognized as not implying direct relationship among such disjunct, modified forms. The best-known examples are to be found in several rodents, where isolated populations occur on disjunct, black lava beds, for instance, *Peromyscus* and *Neotoma* (Benson, 1933; Blair, 1954; Dice, 1941). Even when such discontinuous populations are given the same sub-specific name, it is generally recognized that they are of polyphyletic origin. The data in the present instance, we believe, warrant the more plausible, alternative hypothesis of independent evolution of similar characters, as in the above-mentioned examples. Otherwise, a phylogeny based purely on the morphology of these species, which actually behave geographically as subspecies, would be hard to reconcile with the present distributions of the various forms. We postulate, therefore, a relatively rapid and early expansion of the subgenus into the range it now occupies, with the major portion of its morphological evolution, or diversification, having taken place subsequently.

No conclusions about the taxonomic status of the various named species and subspecies have been drawn, because the material from critical areas is lacking, at least in the American Museum collection. All the populations appear to be allopatric with the possible exception of *A. mitrata* and *A. leucophthalmus* the ranges of which are contiguous or slightly overlapping in the eastern Andes of Peru and Bolivia. They may be ecologically separated in those areas. The most confusing area, from which new discoveries are certain to throw most light on the systematics of these parakeets, is the region comprising southern Colombia, Ecuador, Peru, Bolivia, and extreme western Brazil. It is there that the ranges of *A. mitrata*, *A. wagleri*, *A. erythrogenys*, and *A. leucophthalmus* approximate one another. Clarification of the relationships of *A. wagleri frontata* Cabanis might be of some importance, as its alleged rarity (Chapman, 1926) and characters tending towards *A. erythrogenys* or *A. mitrata* lead one to suspect that the few known specimens are hybrids. *Aratinga leucophthalmus nicefori* de Schauensee (1949), considered by its describer to bridge the gap between *A. leucophthalmus* and *A. finschi*, not only has the red forehead of the latter species, but also a red forehead like that of near-by *A. wagleri*, although it has red and yellow under wing-coverts characteristic of both *A. finschi* and *A. leucophthalmus*.

## CONCLUSIONS AND SUMMARY

It is evident that the Greater Antilles were naturally colonized by the genus *Aratinga* on at least two separate occasions. The first of these incursions was by the ancestors of *A. (Aratinga) euops* and *A. (Aratinga) chloroptera*, perhaps at some early date before the primary differentiation centers had achieved their present-day aspect. Thus the red under wing-coverts of the Greater Antillean birds may represent either parallel evolution with *A. finschi*, *A. erythrogenys*, and *A. leucophthalmus* or retention of a primitive character of the subgenus, rather than being an expression of immediate affinity with any one of those forms. If it be assumed for the moment that *A. euops* and *A. chloroptera* are not specially related to *A. (Aratinga) labati* (the extinct parakeet of Guadeloupe), Mexico or northern Central America could well have been the place of origin of the ancestral stock, but the exact invasion route may never be known.

The place of *A. labati* in this picture is unfortunately obscure. If it had an origin independent of the Cuban and Hispaniolan species, then it is rather probable on geographical grounds that this Lesser Antillean form was derived from South America. Its resemblance to *A. holochlora* must also be interpreted as independent evolution. The possibility exists, however, that all the West Indian members of the subgenus *Aratinga* were derived from a single source. There is no morphological or distributional evidence enabling us to say in this case whether or not this stock reached the Antilles from South or Middle America. The origin or origins of all three West Indian species are therefore very unclear. There is at least no compelling reason to assume a direct relationship of *A. euops* and *A. chloroptera* with *A. leucophthalmus*.

The next colonization of the Greater Antilles was by *A. (Eupsittula) nana* which must have come to Jamaica directly from Middle America. This was probably at a later date than the arrival of the ancestors of *A. euops* and *A. chloroptera*.

*Aratinga (Eupsittula) pertinax* appears to have been introduced on St. Thomas from Curaçao; there is no convincing evidence that it reached the island by natural means, although that is a distinct possibility. A population of *A. pertinax*, presumably unrelated to the population of St. Thomas, is supposed to have once been present on Martinique, but how it might have reached there is presently unsolvable.

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